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The penis of the CHLOROCYPHIDAE (Odonata) as a group-character.
By J. COWLEY, M.A. . . . . pp. 1–18

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TRANSACTIONS

OF THE

ROYAL

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OF LONDON

VOL. 86. 1937.

THE PENIS OF THE CHLOROCYPHIDAE (ODONATA) AS A GROUP-CHARACTER

By J. COWLEY, M.A.

[Read 18th November, 1936.]

WITH SIXTY TEXT-FIGURES.

THIS study was undertaken at the suggestion of Dr. F. F. Laidlaw in order to determine to what extent the penis in the family CHLOROCYPHIDAE (LIBELLAGINIDAE of authors) might afford group-characters; much of the material was kindly presented to me for my collection by Dr. Laidlaw, all species represented in the British Museum (Mr. Kimmins) and Cambridge University Museum (Mr. Kerrich) collections were examined, and Dr. F. C. Fraser supplied penes of *Chlorocypha asiatica* and *C. vittata*; to all of whom I wish to record my indebtedness, and in particular to Dr. Laidlaw who has given me much encouragement and criticism.

The penes were examined in the dried state, and proved to have complicated processes which are difficult to figure adequately as they are twisted and bent in various planes; they can be assigned to ten groups, in some of which (2, 4 and 8) specific differences are probably very slight and difficult to characterise, in other groups (3, 6 and 10) specific differences are well marked; but of the majority of species only one specimen was examined and no attempt was made to estimate any variability in specific details, and, as this study was only intended to give a preliminary grouping, no special effort was made to procure specimens of the rarer species, although it must be admitted that the penis of *Disparocypha* Ris would have been of great interest. Throughout I refrained from studying, either from specimens or in the literature, any other characters (venation, mesothoracic triangle, wing-patterns) on which groups of these insects have been established, in order to minimise any bias towards the accepted

groupings, although I realise that the penis should only be used as a group-character in conjunction with others. For reasons of convenience only, subspecies have been treated binomially as though they were species, no reflection on their taxonomic status being intended. Mr. Kimmins has descriptions of two new species in the press, Dr. Laidlaw of a new species and two new genera. Lest this study should appear before their descriptions are published, the names they are proposing have been omitted here. A general description of the penis of a Chlorocyphid follows :—

Internal and terminal folds present, the third segment normally developed, the apical lateral angles produced as a pair of processes which are probably homologous with the *äusseren Fäden* of Schmidt, 1915 (Agriidae), the *lower penis lobes* of Kimmins, 1933 (*Umma*) and the *oberen Penisfäden* of May, 1935 (*Vestalis*-group), and are here termed the *lateral apical processes*; this pair of processes symmetrically disposed (constantly asymmetrical in certain genera of Agriidae) and directed more or less cephalad and ventrad, frequently spirally twisted. Each lateral apical process may have the mesal and exterior surfaces differentiated into an *internal branch* directed more cephalad and an *external branch* directed more caudad or ventrad; the division into these branches generally somewhat distad to the apical lateral angles of the third segment, marking off an undivided *basal stem* (*see* fig. 55 D), but not always evident when the external branch is not well developed. These internal and external branches may possibly be homologous with the *inner* and *outer branches of the lower penis lobes* found by Kimmins (1933) in *Umma* (cf. *U. cincta*), to which the penis of some forms of *Rhinocypha* bear quite a noticeable superficial resemblance (*e.g.* figs. 53–55); the homology of the external branch with the *Zahn*, *Zapfen* or *Haken* of the *oberen Penisfäden* in the *Vestalis*-group (May, 1935) is perhaps rather more problematical; indeed, these questions of homology of structures which may only be developed in diverse groups (perhaps phylogenetically specialised) must remain in doubt until a more complete knowledge of the general phylogeny and penes of the Zygoptera is available. There are no traces of the *inneren Fäden* of Schmidt, 1915, *upper penis lobes* of Kimmins, 1933, *unteren Penisfäden* of May, 1935, here termed the *median apical processes*. (An alternative scheme would be to homologise the internal branch with the median apical process, the external branch with the lateral apical process of the Agriidae, supposing the division between the two branches to have moved more and more basad and finally to have entirely separated basally as in the typical Agriid condition; but I consider this explanation to be much less probable, for not only do similar branches of the lateral apical process appear to be present in *Umma*, which has the median apical processes also, but in addition the condition in *Chlorocypha*, in which the two branches have become separated, is entirely different from that of the Agriidae, for in the former the internal branch comes to arise *subapically* from the *dorsal surface* of the third segment, whereas in the latter the median apical process is an *apical* continuation of the *margin* of the segment itself.) Spines and hairs on the shaft of the penis were not studied, but generally there are a few very short spines which are scarcely visible.

The chief group-characters are provided by the external and internal branches of the lateral apical processes; variations in the form of the internal and terminal folds and the third segment are slight and do not lend themselves to this purpose, the only exception to the general uniformity found being the excised base of the third segment in *Rhinocypha* sp. (fig. 29 E). It is assumed here that the forms with an undifferentiated external branch are the more primitive,

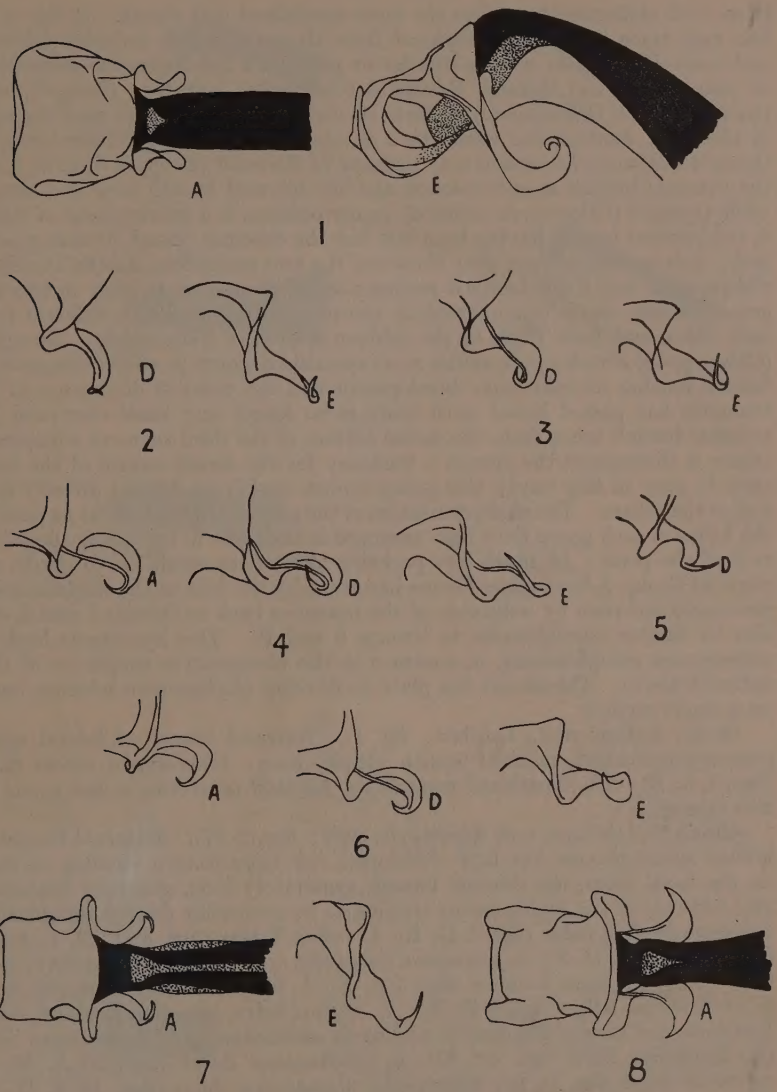


Fig. 1. (*Chlorocypha*) *vittata* Selys. (F.C.F.)
2. *Libellago hyalina* Selys. Baram, Sarawak, ix.1920. (J.C.)
3. *L. indica* Fraser. Fraserpet, Coorg, India, 25.x.1924. (J.C.)
4. *L. finalis* Selys. Kandy, Ceylon, 11.x.1924. (J.C.)
5. *L. semiopaca* Selys. Kuala Tahan, Pahang, 9.xi.1921, F. N. Chasen. (J.C.)
6. *L. aurantiaca* Selys. Phachaung, Tenasserim, 16.ii.1927. (J.C.)
7. *L. greeni* Laidlaw. Paratype; Kandy, Cent. Province, Ceylon, 1.xii.1909, E. E. Green. (B.M.)
8. *L. bisignata* McLachlan. Holotype; Tondano, Menado, Wallace. Saunders coll. (B.M.)

those with elaborated branches the more specialised and recent. If this is so, one may trace lines of development from Group 2, which includes *Libellago* and some *Rhinocypha* species (the latter perhaps a heterogeneous assemblage of primitive forms) through Groups 3 (*Calocypha*) and 4 to Group 7, with Groups 5 and 6 (*Rhinoneura*) as more specialised offshoots from near the apex of this line; another line would be a development of Group 8 from Group 2. Group 1 (*Chlorocypha vittata*) may perhaps be the most primitive form in which the external branch is undeveloped and the internal branch long and simple, while Group 9 (*Chlorocypha asiatica*), in my opinion, is a development of Group 8, the internal branch having been lost and the external branch further specialised; it is worthy of note that these are the two anomalous Asiatic species of *Chlorocypha*, which Dr. Laidlaw proposes on other grounds to place in two new genera, which course is supported by the penes being markedly different from each other and from those of the African species of *Chlorocypha*. Group 10 (*Chlorocypha*) stands apart as the most specialised group in which the external branch reaches its maximum development and the point of divergence of the branches has passed basad until there is no longer any basal stem and the internal branch arises from the dorsal surface of the third segment subapically (there is throughout the groups a tendency for the mesal margin of the basal stem to arise in this way); this group cannot readily be derived directly from any of the others. The characterisation of the groups follows; so far as possible the forms in each group have been arranged in the order of increasing specialisation of the penis. (A much less probable alternative would be to derive the penis of Group 8 from some *Umma*-like form by the loss of the median apical processes, and then by reduction of the branches back to Groups 1 and 2, and also by further specialisation to Groups 9 and 10. This hypothesis leads to unnecessary complications, in contrast to the comparative simplicity of that outlined above. This is not the place to develop phylogenetic schemes based on a single organ.)

Group 1 (Gen. nov., Laidlaw; fig. 1). External branch of lateral apical process not evident, internal branch simple, long: *Chlorocypha vittata* Selys (figs. 1 A, E). On venational grounds Dr. Laidlaw is erecting a new genus for this species.

Group 2 (*Libellago*, and *Rhinocypha* part; figs. 2–17). External branch of lateral apical process but little developed, not more than a swelling or ridge on the basal stem, the internal branch moderately long, generally lanceolate and twisted, in the higher forms tending to be somewhat dilated subapically: *Libellago hyalina* Selys (figs. 2 D, E), *L. indica* Fraser (figs. 3 D, E), *L. finalis* Selys (figs. 4 A, D, E), *L. semiopaca* Selys (fig. 5 D), *L. aurantiaca* Selys (figs. 6 A, D, E), *L. greeni* Laidlaw (figs. 7 A, E), *L. bisignata* McLachlan (fig. 8 A), *L. snellemanni* Selys (figs. 9 D, E); *L. stictica* Selys, *phaethon* Laidlaw, *mima* Lieftinck and *lineata* Burmeister similar to *snellemanni*; *L. stigmatizans* Selys (*cf.* Kennedy, 1920, figs. 80, 81), *L. xanthocyana* Selys (figs. 10 A, E), *L. rufescens* Selys (fig. 11 D), *Rhinocypha unimaculata* Selys (figs. 12 A, D, E), *R. terminata* Selys (figs. 13 A, D, E, J), *R. iridea* Selys (figs. 14 D, F), *R. ignipennis* Selys (figs. 15 A, D), *R. trimaculata* Selys (figs. 16 A, D, E, G), *R. pagenstecheri* Förster (figs. 17 A, B, D, E, J). It may be doubted whether all these heterogeneous *Rhinocypha* species belong to this group, but they appear to agree better with the majority of this group than any other; the *Libellago* species studied undoubtedly all fall into one group.

Group 3 (*Calocypha*; figs. 18, 19). External branch of lateral apical process but little developed, internal branch shorter and broader, scarcely twisted,

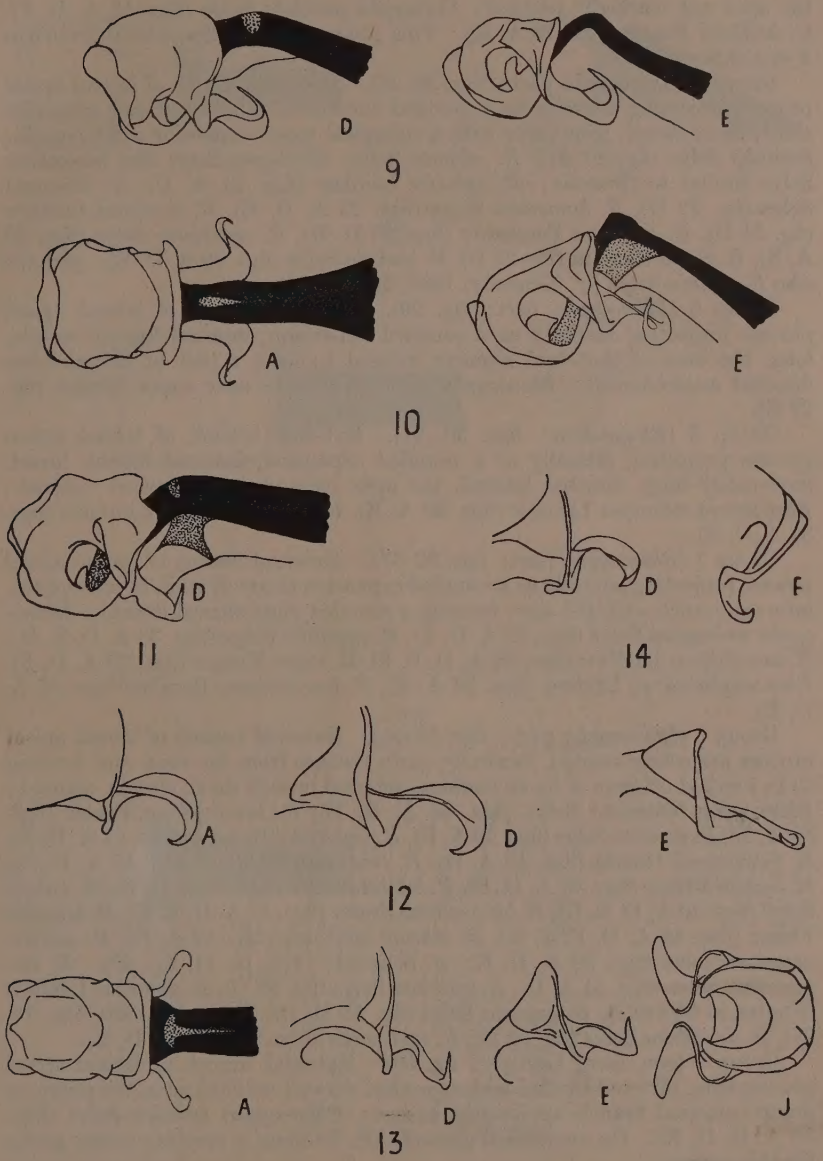


FIG. 9. *L. snellemanni* Selys. Benkoelen Distr., Sumatra, C. J. Brooks. (B.M.)
10. *L. xanthocyana* Selys. Celebes. (B.M.)
11. *L. rufescens* Selys. HOLOTYPE; Celebes or Mindanao. Saunders coll. (B.M.)
12. *Rhinocypha unimaculata* Selys. Simla, India. (J.C.)
13. *R. terminata* Selys. Amboina, E. Indies, F. Muir. (U.M.Z.C.)
14. *R. iridea* Selys. Maymyo, Upper Burma, 16.xi.1924. (J.C.)

the apex not markedly pointed: *Calocypha petiolata* Selys (figs. 18 A, E, F), *C. laidlawi* Fraser (figs. 19 A, E). This group might perhaps be included in 2 as a subgroup.

Group 4 (*Rhinocypha* part; figs. 20–28). External branch of lateral apical process projecting laterally as a rounded expansion, internal branch generally short, fairly broad, sometimes with a subapical mesal expansion: *Rhinocypha frontalis* Selys (fig. 20 A); *R. colorata* Selys, *albistigma* Selys and *monochroa* Selys similar to *frontalis*; *R. spinifer* Laidlaw (figs. 21 A, D), *R. bisignata* Selys (fig. 22 D), *R. humeralis* Selys (figs. 23 A, D, E), *R. moultoni* Laidlaw (fig. 24 D), *R. perforata* Percheron (figs. 25 D, H), *R. semitincta* Selys (figs. 26 A, E), *R. tincta* Rambur (fig. 27 D), *R. limbata* Selys (figs. 28 A, D, E); perhaps also *R. eximia* Selys (*cf.* Kennedy, 1920, figs. 78, 79).

Group 5 (*Rhinocypha* part; fig. 29). External branch of lateral apical process projecting laterally as a rounded expansion, internal branch simple, long, the base of the third segment excised to form a pair of lateral lobes directed caudo-dorsad: *Rhinocypha* sp. n. Kimmins, near *stygia* Förster (fig. 29 E).

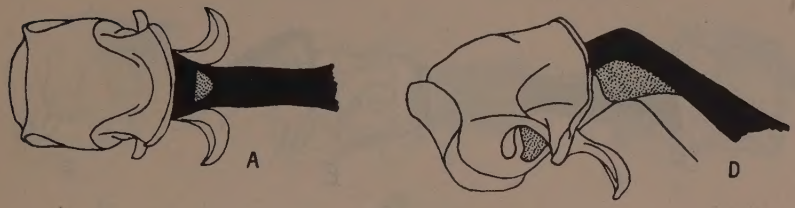
Group 6 (*Rhinoneura*; figs. 30, 31). External branch of lateral apical process projecting laterally as a rounded expansion, internal branch broad, moderately long, directed laterad, the apex expanded and turned ventrad: *Rhinoneura villosipes* Laidlaw (figs. 30 A, E), *Rhinoneura* sp. n. Kimmins (figs. 31 A, C, E).

Group 7 (*Rhinocypha* part; figs. 32–37). External branch of lateral apical process projecting laterally as a rounded expansion (scarcely so in *R. anisoptera*), internal branch with the apex forming a rounded plate turned dorsad: *Rhinocypha anisoptera* Selys (figs. 32 A, D, F), *R. cucullata* Selys (figs. 33 A, D, E, H), *R. aurofulgens* Laidlaw (figs. 34 A, D, E, F), *R. selysi* Krüger (figs. 35 A, D, F), *Rhinocypha* sp. n. Laidlaw (figs. 36 A, E), *R. heterostigma* Rambur (figs. 37 A, D, E).

Group 8 (*Rhinocypha* part; figs. 38–55). External branch of lateral apical process projecting caudad, ventrally quite distinct from the stem and tending to be marked off from it by an excision, internal branch short, simple, pointed: *Rhinocypha bifasciata* Selys (figs. 38 A, D, E), *R. hemihyalina* Fraser (figs. 39 A, E), *R. cuneata* Selys (figs. 40 A, E), *R. fenestrella* Rambur (figs. 41 A, D, E), *R. fulgipennis* Guérin (figs. 42 A, D), *R. fenestrata* Rambur (figs. 43 A, D, E), *R. beesoni* Fraser (figs. 44 A, D, E), *R. biforata* Selys (figs. 45 A, D, E), *R. spuria* Selys (figs. 46 A, D, E, G), *R. bifenestrata* Fraser (figs. 47 A, D, E, F), *R. hilaryae* Fraser (figs. 48 A, D, E, J, K), *R. mariae* Lieftinck (figs. 49 A, D), *R. quadrimaculata* Selys (figs. 50 A, D, E; *cf.* Schmidt, 1915, pl. 11, fig. 49). *R. immaculata* Selys (figs. 51 A, D), *R. biseriata* Selys (fig. 52 D), *R. anambae* Laidlaw (similar to *biseriata*), *R. angusta* Selys (fig. 53 D; *cf.* Kennedy, 1920, figs. 76, 77), *R. delimbata* Selys (fig. 54 D), *R. trifasciata* Selys (figs. 55 A, D, E).

Group 9 (gen. nov., Laidlaw; fig. 56). External branch of lateral apical process long, directed caudad and somewhat dorsad, notched as in the previous group, internal branch apparently absent: *Chlorocypha asiatica* Selys (figs. 56 A, B, D, E). On venational grounds Dr. Laidlaw is erecting a new genus for this species.

Group 10 (*Chlorocypha*; figs. 57–60). External branch of lateral apical process large, strap-shaped, extending markedly dorsad, basal stem of the process absent, internal branch arising from the dorsal surface of segment 3 subapically, long, the apex more or less expanded and sometimes turned ventrad: *Chlorocypha selysi* Karsch (figs. 57 A, E, J); *C. rubida* Selys, *curta* Selys and



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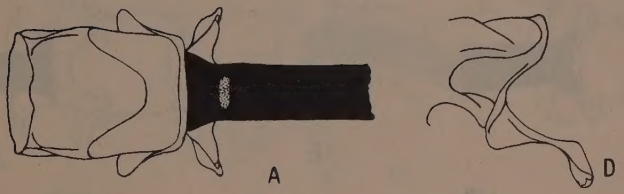

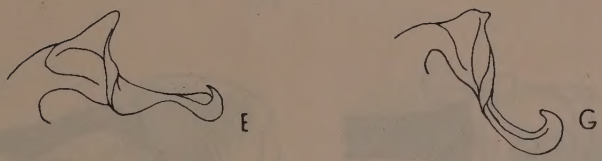

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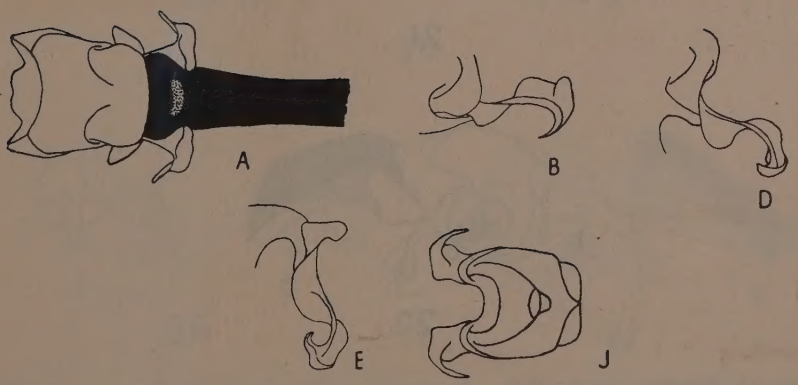

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Fig. 15. *R. ignipennis* Selys. Shillong, Assam, H. M. Parish. (B.M.)
16. *R. trimaculata* Selys. Khasi Hills, Assam. (J.C.)
17. *R. pagenstecheri* Förster. Lombok, 1,500 ft., v.1896, Everett. (U.M.Z.C.)

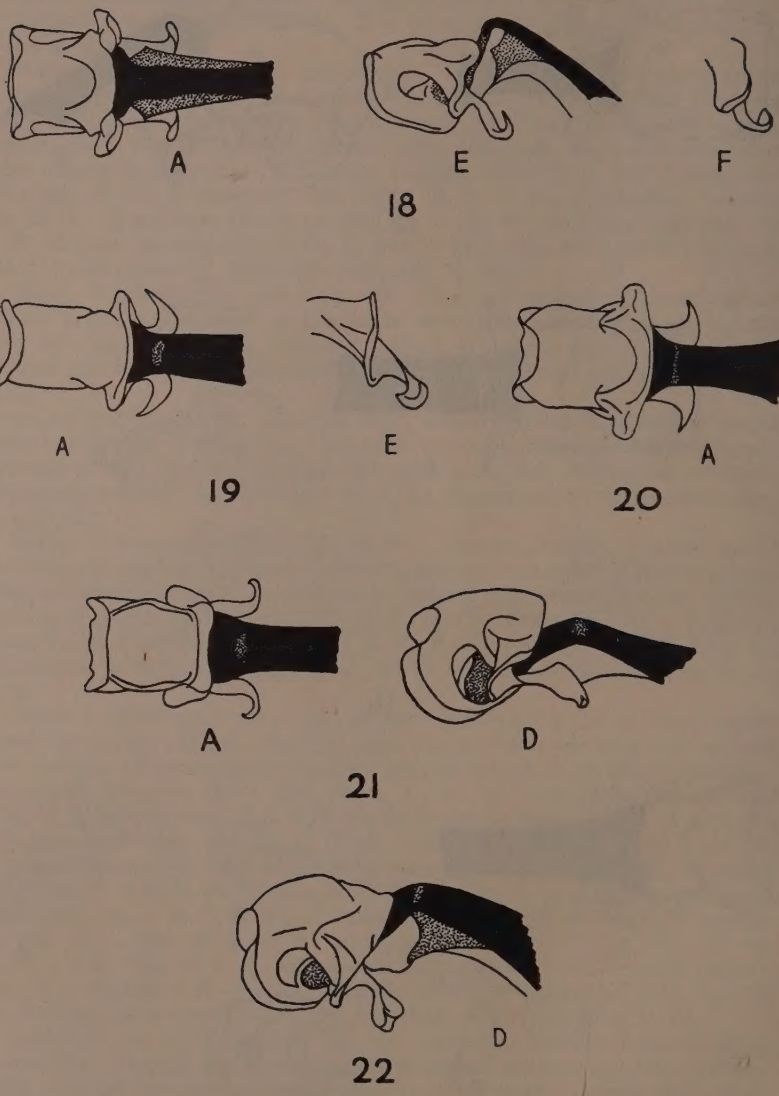
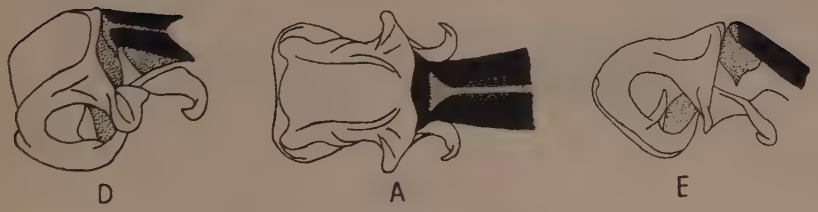


Fig. 18. *Calocypha petiolata* Selys. Bengkajang, nr. Singkawang, W. Borneo, 21.iv.1932, Coomans de Ruiter. (J.C.)
19. *C. laidlawi* Fraser. Sampaji, Coorg, India, 8.xii.1924, F. C. Fraser. (B.M.)
20. *Rhinocypha frontalis* Selys. Shortland Is. (B.M.)
21. *R. spinifer* Laidlaw. R. Koyan, 2,500 ft., Mt. Dulit, Sarawak, 17.xi.1932, B. M. Hobby & A. W. Moore. (B.M.)
22. *R. bisignata* Selys. Khandala, India, 7.iv.1920, F. C. Fraser. (B.M.)



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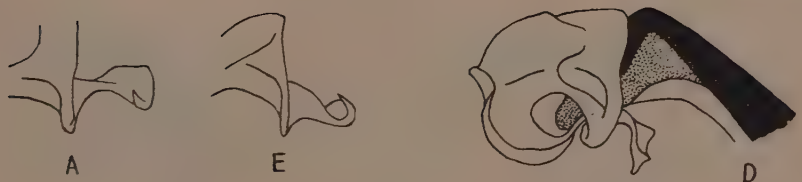

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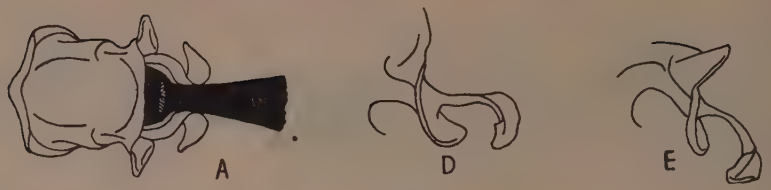
FIG. 23. *R. humeralis* Selys. Balaboe. (J.C.)
24. *R. moultoni* Laidlaw. HOLOTYPE; Kinabalu, Borneo, I.x.1913, J. C. Moulton. (B.M.)
25. *R. perforata* Percheron. Mt. Wuchi, Hainan, 21.v.1903. (B.M.)
26. *R. semitincta* Selys. Gizo Is., A. S. Meek. (J.C.)
27. *R. tincta* Rambur. New Guinea, Wallace. (B.M.)



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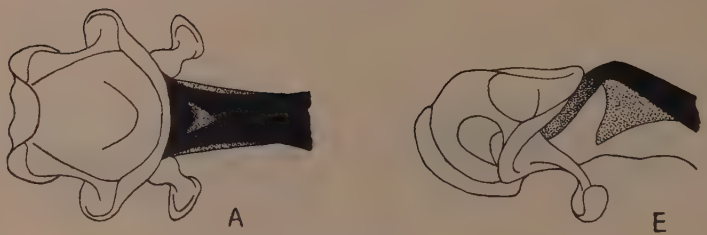

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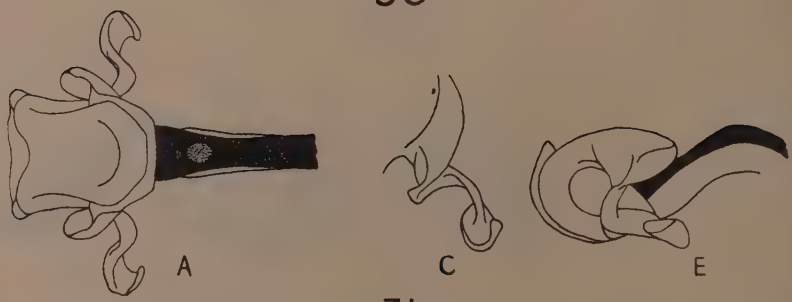

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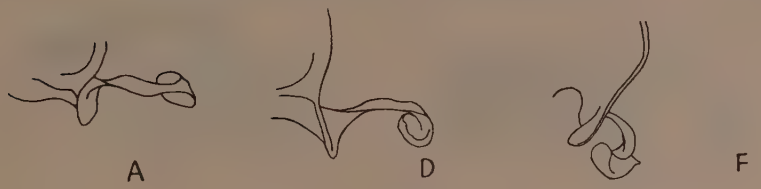
FIG. 28. *R. limbata* Selys. PARATYPE of *R. inas* Laidlaw; Gunong Inas, Malay Peninsula, Skeat Expedition. (U.M.Z.C.)

29. *Rhinocypha* sp. n. Kimmins. PARATYPE; Dulit Trail, Mt. Dulit, Sarawak, 10.viii.1932, B. M. Hobby & A. W. Moore. (B.M.)

30. *Rhinoneura villosipes* Laidlaw. HOLOTYPE; Kinabalu, Borneo, 6.ix.1913, J. C. Moulton. (B.M.)

31. *Rhinoneura* sp. n. Kimmins. HOLOTYPE; Mt. Dulit, 4,000 ft., Sarawak, 22.x.1932, B. M. Hobby & A. W. Moore. (B.M.)



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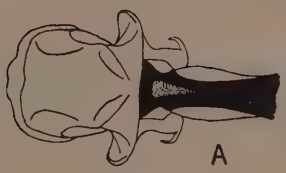

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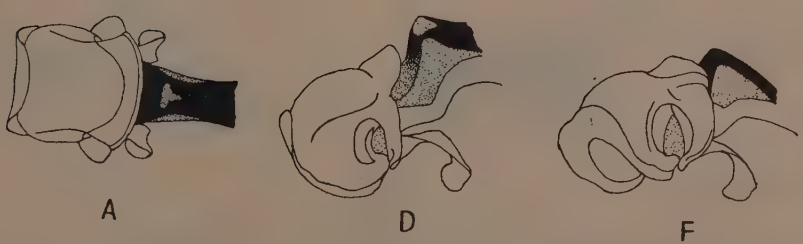

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FIG. 32. *Rhinocypha anisoptera* Selys. Malang, E. Java, ix–x.1929, S.O. (J.C.)
33. *R. cucullata* Selys. Madalam, Sarawak, 15.ii., H. W. Smith. (J.C.)
34. *R. aurofulgens* Laidlaw. Lewpin Aga House, 7.x.1920. (J.C.)
35. *R. selysi* Krüger. Setinjak, Philippine Is. (! *recte* Sumatra), 1,800 ft. (B.M.)

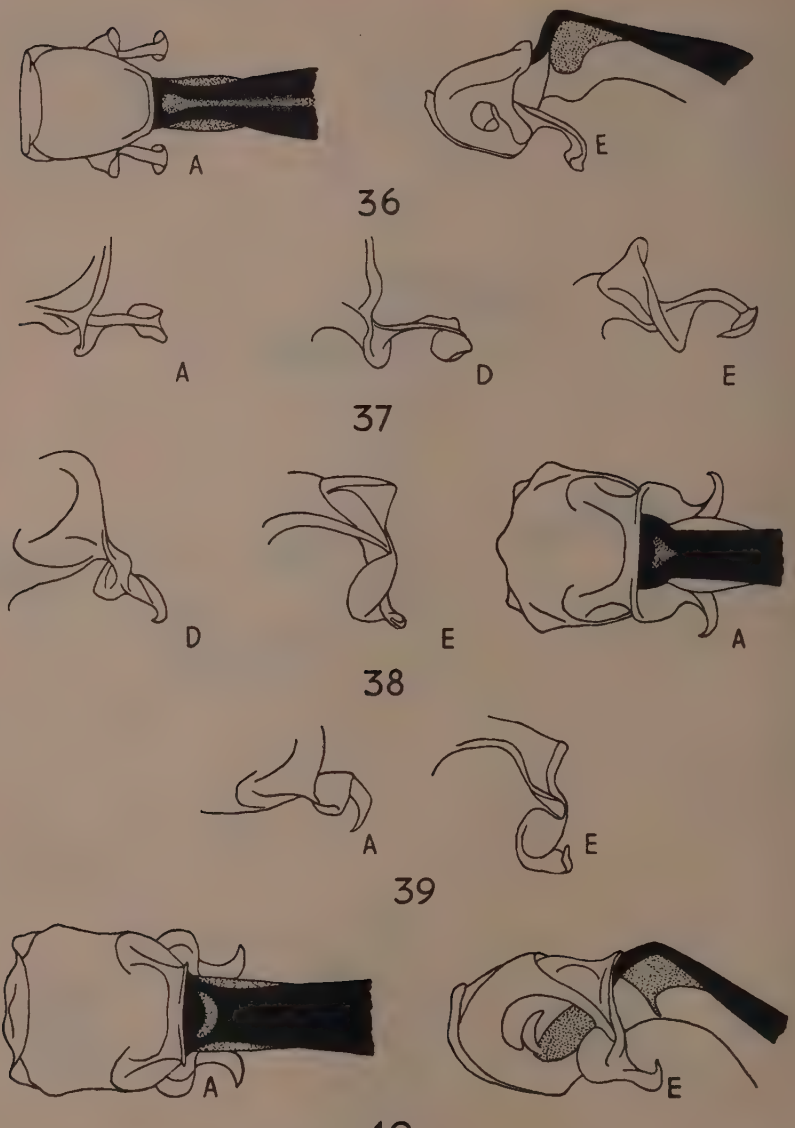


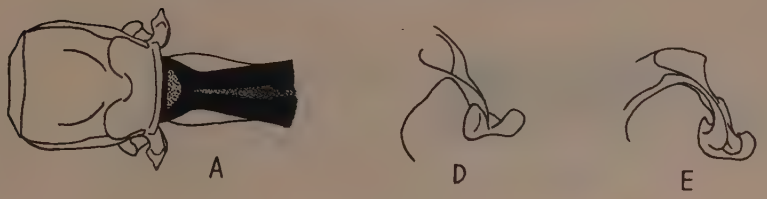
Fig. 36. *Rhinocypha* sp. n. Laidlaw. Holotype; Gunong Kledang, Perak, 2,646 ft., xi.1916. (B.M.)

37. *R. heterostigma* Rambur. Batorraden, Java (?), 18.xii.1927. (J.C.)

38. *R. bifasciata* Selys. Mungpoo, Darjeeling Distr., 4,000 ft., India, 19.xi.1924. (J.C.)

39. *R. hemihyalina* Fraser. Holotype; Khasi Hills, Shillong, 16.x.1919, Fletcher. (B.M.)

40. *R. cuneata* Selys. Sikkim. Crowley bequest. (B.M.)



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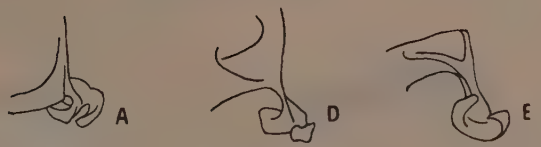

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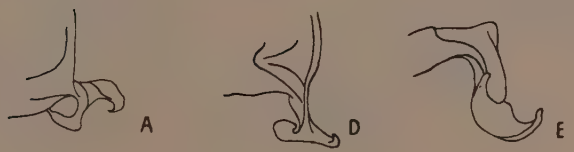

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Fig. 41. *R. fenestrella* Rambur. Malay Peninsula, Skeat Expedition. (U.M.Z.C.)
42. *R. fulgipennis* Guérin. Daban, Phanrang Prov., S. Annam, 650 ft., 1918, Malcolm A. Smith, C. Boden Kloss. (B.M.)
43. *R. fenestrata* Rambur. Ranu Lamongan, Klakah, E. Java, x–xi.1928, A. Thienemann. (J.C.)
44. *R. beesoni* Fraser. Mergui, Lower Burma, Bott. (J.C.)
45. *R. biforata* Selys. Catchment area nr. Jitra, India, 10.iv.1928. (J.C.)

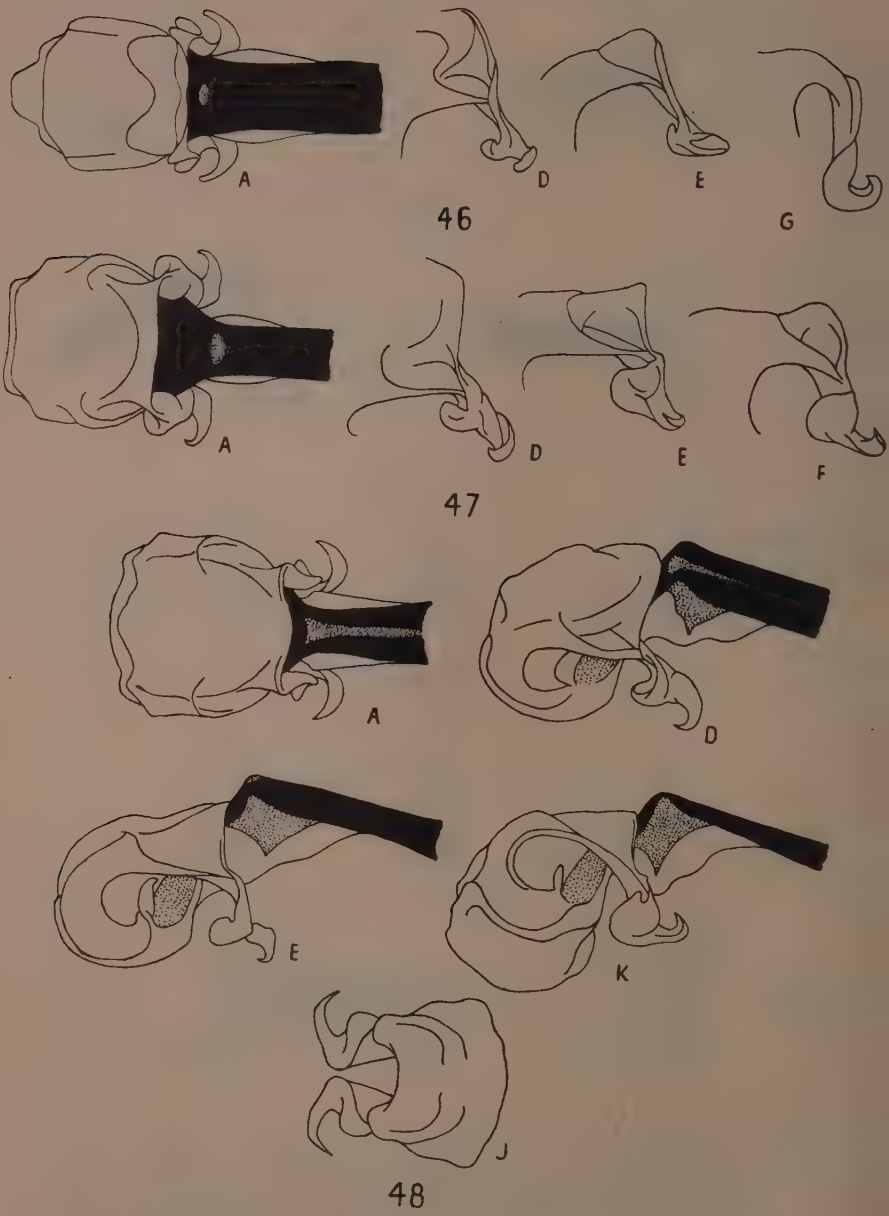

Fig. 46. *R. spuria* Selys. Khasi Hills, Assam. (J.C.)
47. *R. bifenestrata* Fraser. Moungpoo, Darjeeling Distr., India, 25–29.v.1927. (J.C.)
48. *R. hilaryae* Fraser. Paratype; Maymyo, Upper Burma, 19.vi.1924, F. Wall. (J.C.)

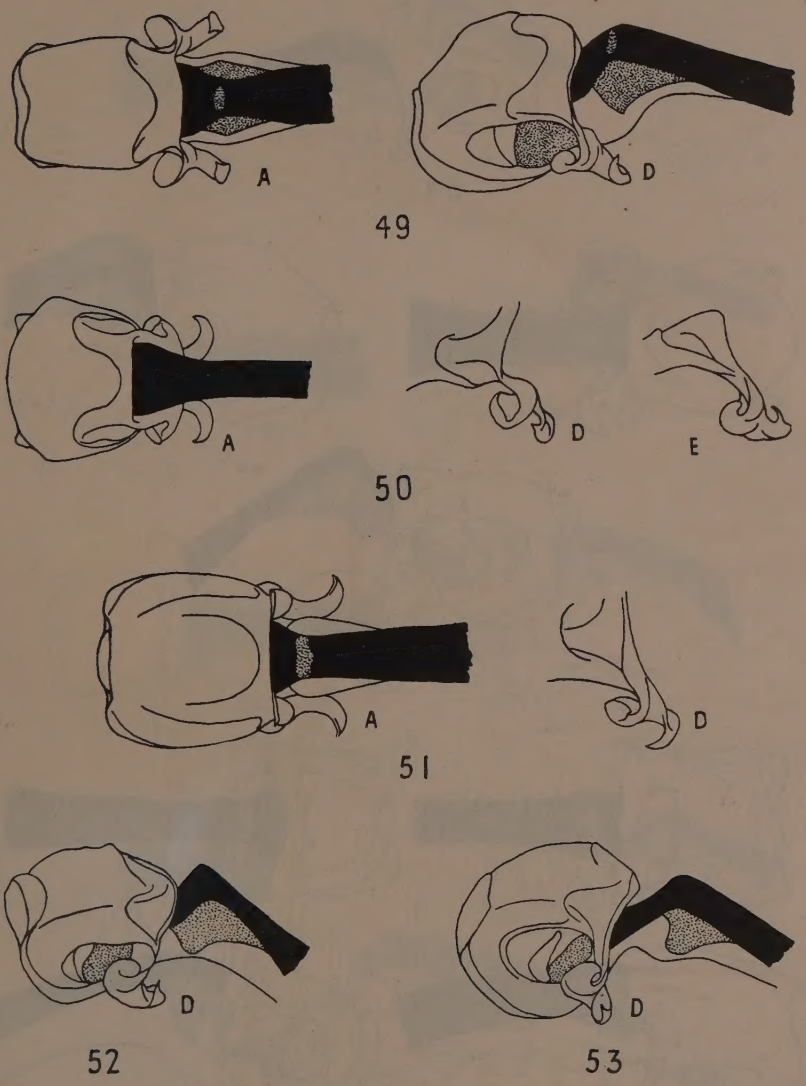

FIG. 49. *R. mariae* Lieftinck. Wai Panas, Ranau See, S. Sumatra, 4.ii.1929, A. Thienemann. (B.M.)
50. *R. quadrimaculata* Selys. Cherrapunji, Khasi Hills, Assam. (J.C.)
51. *R. immaculata* Selys. Cherrapunji, 4,900 ft., Assam. (I.M.)
52. *R. biseriata* Selys. Kinabalu, Borneo. (B.M.)
53. *R. angusta* Selys. Setinjak, Sumatra, 1,800 ft., i.1898, Ericson leg. (B.M.)

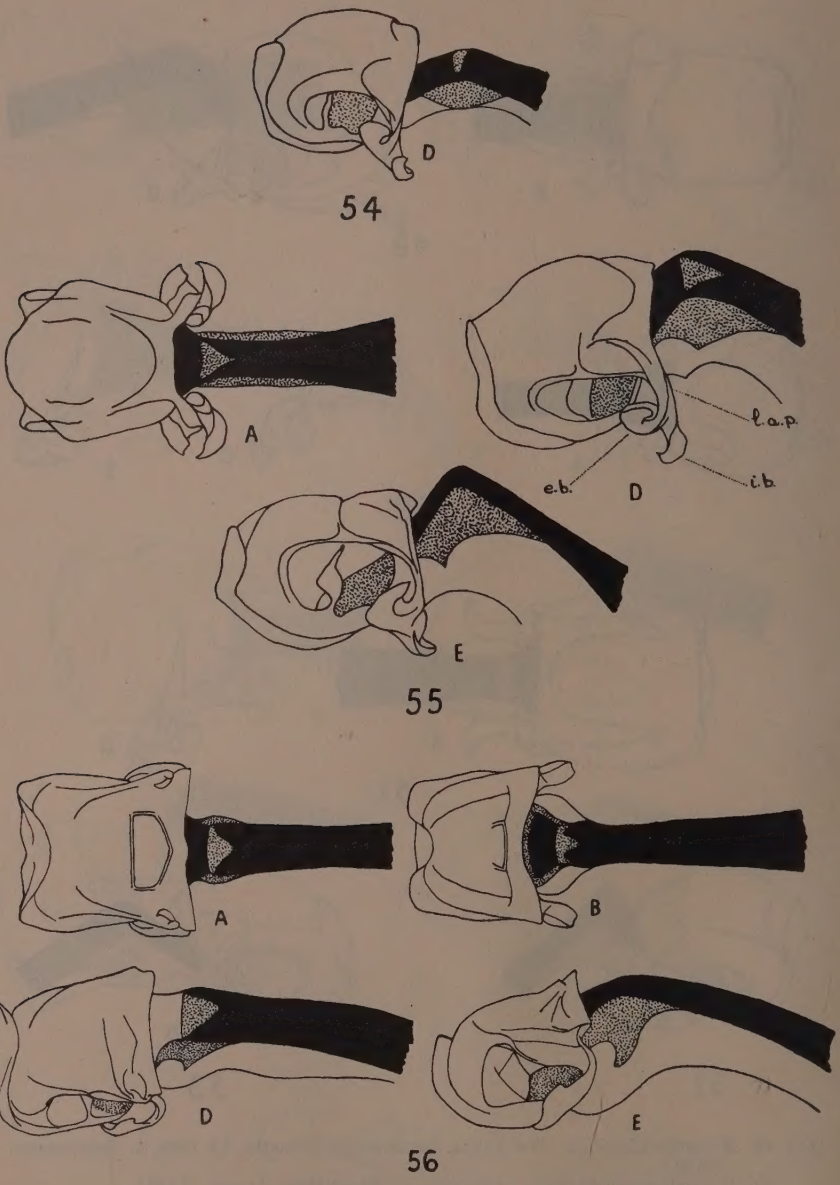

Fig. 54. *R. delimbata* Selys. Basin of Fleuve Rouge, Thai-Nien, Tonkin, 19.iii.1924, H. Stevens. (B.M.)

55. *R. trifasciata* Selys. N. India. (B.M.). *l.a.p.*: basal stem of lateral apical process; *i.b.*: internal branch; *e.b.*: external branch.

56. (*Chlorocypha*) *asiatica* Selys. (F.C.F.)

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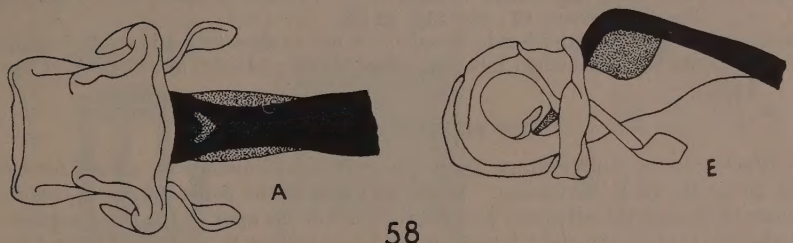

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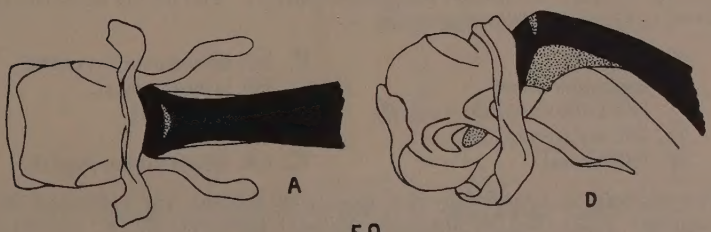

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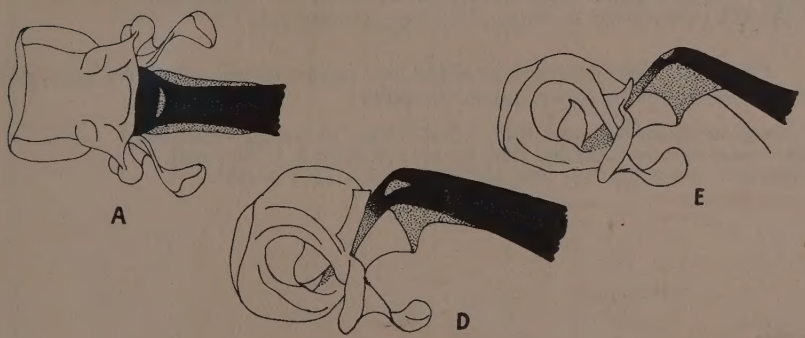

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FIG. 57. *Chlorocypha selysi* Karsch. Santa Isabel, Fernando Po, 24.iii.1904. (B.M.)
58. *C. jejuna* Baumann. Chirinda For., Gazaland, 3,600 ft., 17.x.1905, G. A. K. Marshall. (B.M.)
59. *C. dispar* Beauvois. Edijar, Ashanti, E. Coast, 31.i.1913, J. J. S. (B.M.)
60. *C. caligata* Selys. Pietermaritzburg, Natal. (J.C.)

glaucifrons Sjöstedt similar to *selysi*; *Chlorocypha* sp. (Schmidt, 1915, pl. 11, fig. 48), *C. jejuna* Baumann (figs. 58 A, E), *C. dispar* Beauvois (figs. 59 A, D), *C. caligata* Selys (figs. 60 A, D, E; *cf.* Kennedy, 1920, figs. 74, 75).

References.

Kennedy, C. H., 1920, The phylogeny of the Zygopterous Dragonflies as based on the evidence of the penes. *Ohio J. Sci.*, **21**: 19–29, 3 pls.

Kimmins, D. E., 1933, The form of the penis as a group-character in the genus *Umma*, Kirby (Odonata). *Stylops*, **2**: 140–144, 14 figs.

May, E., 1935, Über die Genera *Vestalis* Selys, *Vestinus* Kennedy und *Vestalaria* n.g. *Senckenbergiana*, **17**: 207–218, 22 figs.

Schmidt, E., 1915, Vergleichende Morphologie des zweiten und dritten Abdominalsegments bei männlichen Libellen. *Zool. Jahrb.*, (*Anat.*), **39**: 87–200, 24 figs., 3 pls.

Descriptions of Figures.

Penes of Chlorocyphidae, from camera lucida drawings by myself (except fig. 29 by Mr. D. E. Kimmins). When only part of the penis is figured, it is the whole of the left lateral apical process and part of the apex of the third segment. Although part of the right lateral apical process may be visible in lateral and semilateral views, it is omitted for greater clarity. The letters after the figure-numbers indicate the following views :—

A. ventral.
B. cephalo-ventral.
C. left latero-cephalo-ventral.
D. left latero-ventral.
E. left lateral.
F. left latero-caudo-ventral.
G. left latero-caudal.
H. caudo-ventral.
J. caudal.
K. left latero-dorso-caudal.

The collections containing the specimens figured are indicated by abbreviations: B.M. (British Museum, Natural History), F.C.F. (collection of Dr. F. C. Fraser), I.M. (Indian Museum, Calcutta), J.C. (collection of the author), U.M.Z.C. (University Museum of Zoology, Cambridge).

Postscript.—The descriptions of the new species mentioned above have been published while this paper was in the press :

Rhinocypha cognata Kimmins, 1936, *J.F.M.S.Mus.*, **18**: 84, fig. 8 (Sarawak).
Rhinoneura caerulea Kimmins, 1936, *loc. cit.* : 79, fig. 6 A, C (Sarawak).
Rhinocypha pelops Laidlaw, 1936, *loc. cit.* : 60, pl. I, fig. 1 (Perak).